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by

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16. ABSTRACT

Variation in metabolic responses to sulfur dioxide is widespread within many plant species. Plant responses are a consequence of a series of biochemical and physiological events beginning with SO2 flux into plant and progressing through perturbation, and homeostasis, and ending with foliar injury and/or effects on growth and yield. Gas-phase and liquid-phase conductance are important determinants of SO2 flux. However, the relationship between variation in these factors and plant response is incompletely understood-- at least in part because of difficulties with SO2 gas-exchange methodology. Perturbation events occurring primarily in the chloroplast, and homeostatic mechanisms have received only brief attention. The entire sequence of plant response to SO2 needs additional investigation especially to identify components useful in genetic studies of SO2 resistance. Evidence to date demonstrates the heritability of SO2 resistance in both native and cultivated vegetation. Understanding the mechanism for variability in plant response would improve success of breeding for resistance to SO2 injury.

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Intraspecific Variability in Metabolic Responses to SO_2

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Page

Leaf Conductance

Gas-phase conductance.

Methodology for gas-phase studies.

Variability in boundary layer conductance and $J_{surface}$.

Variability in stomatal conductance.

Variability in J_{total} and $J_{internal}$.

Sulfur enrichment.

Liquid-phase conductance.

Perturbation

Homeostasis

Injury

Importance of Metabolic Variability

Summary

Table 1, p.

Table 2, p.

Table 3, p.

Table 4, p.

Table 5, p.

Figure 1, p.

Figure 2, p.

Figure 3, p.

Vegetation responses to air pollutants may range from subtle changes in cellular processes to modifications of whole-plant physiology, visual injury, and/or altered productivity. Without regard to the plant organizational level at which the response is measured, phytotoxicity involves molecular events that culminate in perturbed cellular structure and function. Variable plant response to a given SO_2 level is related to differences in environmental conditions and genic expression. The interaction between the genome and environment is the ultimate source of plant variation in response to SO_2, while the immediate cause is differing physiological states.

Variation in plant response to SO_2 is common and occurs at various levels of plant organization. Intraspecific or differential cultivar sensitivity to SO_2 as determined by foliar injury responses frequently has been used to make inferences about metabolic and growth processes. The injury symptoms result from a series of physiological events occurring before, during, and after exposure which are influenced by genic and environmental factors. Numerous reports documenting differential foliar injury for a wide range of crops, other herbaceous plants, and trees are summarized in Table 1.

A wide range of response was observed in most species even when only a few (2-3) plant selections were examined. In species such as Ilex aquifolium (Brennan and Leone, 1970) where differences were not observed, the inclusion of additional plant selections or higher SO_2 concentrations may have produced responses large enough for reliable detection. In some species such as Lolium perenne (Horsman et al., 1978, Ayazloo and Bell, 1981) or Zea mays (Grzesiak, 1979), significant cultivar differences in growth or yield occurred without apparent differences in foliar injury. To reduce the possible confounding influences of different environmental conditions or developmental phases, individuals of all plant selections that are to be compared must be exposed

simultaneously under the same conditions. Unless this condition is satisfied it is not possible to attribute differential responses to underlying genic characteristics.

To illustrate why plants exhibited variable responses to O_3, Tingey and Taylor (1982) developed a conceptual model of its effects on plant metabolic processes. The basic concepts are also applicable to SO_2; therefore, the model is used here to assist in summarizing and interpreting data (Fig. 1). Plant responses to SO_2 may be viewed as the consequence of a series of biochemical and physiological events beginning with SO_2 uptake and ending with foliar injury and/or effects on growth and yield. The biochemical and physiological processes may be influenced by environmental or genic conditions. The proposed model includes pollutant uptake, perturbation, homeostasis, and injury which may be equated with or result in foliar injury. The model can be summarized as follows:

LEAF CONDUCTANCE: Sulfur dioxide phytotoxicity results from biochemical reactions within the leaf interior. Thus, a primary factor controlling injury is the rate at which SO_2 diffuses from the ambient air into the cellular perturbation sites. Following sorption onto the moist cell surfaces, the pollutant distribution within the leaf and cell is influenced by liquid phase reactions including diffusion, formation of derivatives, and reactions with scavenging systems.

PERTURBATION: Consists of alterations induced by SO_2 in cell structure and/or function. The initial phytotoxic response probably results from the reaction of SO_2 or its derivatives with macromolecules that are instrumental for the maintenance of cell function.

HOMEOSTASIS: The recovery processes that occur following the perturbation event. These cellular processes may be either repair or compensatory responses.

INJURY: Cellular changes that are the consequence of the series of events following pollutant exposure. The injury is controlled by the interplay between leaf conductance, perturbation, and the extent to which homeostatic processes are able to repair, restore, or compensate for cellular dysfunctions.

Leaf Conductance

Sulfur dioxide uptake (flux) is controlled by the physical and chemical properties of the pathway with physical properties predominant for the initial gas-phase flux into the leaf; chemical properties are predominant for subsequent liquid-phase flux into cells (Fig. 2). Sulfur dioxide flux is usually modeled with the same analog model assumptions and approach used to describe CO_2 uptake and H_2O vapor loss. Therefore, SO_2 flux (J_{SO_2}) into the leaf is proportional to the SO_2 concentration gradient between the atmosphere (Ca) and the leaf interior (Ci); as well as the pathway conductance for SO_2 (g) where:

$$J_{SO_2} = (Ca - Ci) * g \qquad (1)$$

This relationship between conductance (resistance^{-1}) and flux has frequently been used to model air pollution fluxes into leaves (e.g., Tingey and Taylor, 1982; Black and Unsworth, 1979a; Unsworth et al., 1976; Winner and Mooney, 1980a).

Conductance can be partitioned into various components, i.e., boundary layer (g_a), stomatal (g_s), and residual (g_r, also termed mesophyll, internal, or chemical, among others). Boundary layer conductance influences the

fraction of the gas-phase flux diffusing to the leaf surfaces ($J_{surface}$). Stomatal conductance determines the fraction of the total gas-phase flux that passes through the stomatal pore into the substomatal cavity. Residual conductance includes components of diffusion distance and chemical reactivity, and it affects the liquid-phase flux from the substomatal cavity into the mesophyll cells. The stomatal and residual conductance jointly determine flux to the active sites within cells ($J_{internal}$).

Gas-phase conductance. Many studies have focused on variability in gas-phase conductance as the primary mechanism for differential plant response to SO_2. However, these studies produced conflicting results with some indicating that differential injury responses were correlated with the gas-phase conductance of SO_2, whereas no correlation was observed in others (Table 2). These divergent conclusions may, in part, stem from actual differences in gas-phase conductance within or among species, or also may result from errors in basic assumptions and the experimental procedures used to determine gas-phase conductance and SO_2 uptake.

Because experimental methodology has a major impact on data interpretation, the various approaches will be briefly examined. Plant uptake of SO_2 can be determined either by measuring the removal of sulfur from the atmosphere or, antithetically, by determining sulfur enrichment of the plant during exposure. Both approaches have inherent difficulties in experimental procedures and interpretation of results. However, with careful delineation of the implicit assumptions and experimental methods, both approaches can provide useful information. Because the two types of studies differ in basic approach, their methodologies will be considered separately.

Methodology for gas-phase studies. Sulfur dioxide flux may be determined either by direct measurement or by calculation. The latter method from

concentration gradient and conductance measurements for SO_2 or H_2O with appropriate adjustments made for differences in diffusivity according to equation (1).

Direct determination of SO_2 flux by the mass balance approach (e.g., Winner and Mooney, 1980a; Taylor and Tingey, 1981), is determined by the equation:

$$J_{SO_2} = ([SO_2]_{in} - [SO_2]_{out})\ F*A^{-1} \qquad (2)$$

The required measurements include (i) SO_2 concentration in the air before and after it passes over the plant, (ii) air flow rate (F) through the chamber, and (iii) amount of plant material (A), usually leaf area but dry weight is also used. The measured difference between the SO_2 concentration in and out of the gas-exchange chamber represents the SO_2 sorbed by the plant and the experimental system. Thus, accurate measurement of SO_2 loss to the system (primarily to the exposure chamber or cuvette) is required for calculation of actual SO_2 flux to the plant. Losses to the system are influenced by factors such as dewpoint (Taylor and Tingey, 1979), type of chamber surfaces and the amount of time SO_2 has been in the system. Therefore, determination of SO_2 losses to the system must be made under conditions identical to those when a plant is present. For example, to accurately determine chamber sorption, the dewpoint of the air in the chamber must be maintained at the same level as when the plant is present and actively transpiring. If system losses are not properly determined, caution is required when evaluating SO_2 flux to the plant.

Total SO_2 flux (J_{total}) to the plant represents the sum of the SO_2 adsorbed onto the leaf surface ($J_{surface}$) and absorbed into the leaf interior ($J_{internal}$). Generally, it has been assumed that $J_{surface}$ has no physiolog-

ical role, and that only $J_{internal}$ induces plant responses (Runeckles, 1974; Winner and Mooney, 1980a). However, both $J_{surface}$ and $J_{internal}$ are important in evaluating gas-phase flux to plants.

If $J_{surface}$ is large or boundary layer conductance is small, the effective SO_2 concentration at the stomatal pore will be reduced compared to the bulk air. Therefore, the measured SO_2 concentration in the air may not accurately reflect either the concentration gradient through stomata into the leaf, or the concentration affecting cells inside the leaf which is of prime interest in metabolic studies (Runeckles, 1974; Unsworth, 1982). This may be a significant problem as estimates of $J_{surface}$ approach 10-60% of the total SO_2 sorbed by the plant (Spedding, 1969; Garsed and Read, 1974; Fowler, 1978; Elkiey and Ormrod, 1980b, 1981b; Taylor and Tingey, 1981).

Determination of $J_{surface}$ is either by (i) direct measurement of J_{total} when stomata are assumed to be closed and therefore $J_{internal}$ is negligible, or (ii) by subtraction of $J_{internal}$ from J_{total} when $J_{internal}$ is usually derived from analogy to H_2O vapor. Direct measurement of J_{total} is usually made by measuring SO_2 uptake by plants in the dark (Elkiey and Ormrod, 1980b; Tingey and Taylor, 1981); however, problems may arise if either the stomata are not closed or they open in response to SO_2 (Mansfield and Majernik, 1970; Majernik and Mansfield, 1970; Elkiey et al., 1982). Possible dark stomatal opening may be assessed by comparison to nonexposed plants, or to flux measurements in the light. Procedures to insure stomatal closure such as elevated atmospheric CO_2 levels (Raschke, 1975a, b) or ABA treatments (Mittelheuser and van Steveninck, 1971; Raschke, 1975b) also may be used. Calculation of $J_{surface}$ by subtraction of $J_{internal}$ from J_{total} assumes that SO_2 diffusion is controlled by the same processes and follows the same diffusion pathway as H_2O vapor because it utilizes the diffusion of H_2O vapor

as a surrogate for SO_2 (Winner and Mooney, 1980a). The only required adjustment is a correction for differences in diffusivity. In addition, the total H_2O vapor flux from the plant during the light is assumed to be through the stomata, and H_2O vapor flux through the cuticle is generally neglected, even through cuticular transpiration may be large.

Water vapor flux from leaves has been widely used as a surrogate for the flux of SO_2 and other gases into leaves. For example, H_2O vapor flux was used to make inferences about SO_2 uptake in nearly all of the studies listed in Table 2. Water vapor flux may be determined using a gas-exchange chamber or porometry where a humidity sensor is placed near the leaf. Both procedures measure the amount of H_2O vapor diffusing from a leaf or plant to calculate stomatal conductance to H_2O vapor, which may represent conductance for SO_2 once differences in gas diffusivity for the two gases are reconciled. The adjusted stomatal conductance values and the ambient concentration of SO_2 are used in equation (1) to calculate SO_2 flux. The use of H_2O vapor flux to estimate SO_2 uptake has several problems, including: (i) the possibility that SO_2 does not follow the same diffusive pathway as H_2O vapor, (ii) presence of chemical or other internal (residual) factors not present for H_2O vapor which may affect conductance for SO_2, (iii) the lack of consideration of boundary layer conductance if porometry is used, and (iv) the requirement for estimating $J_{surface}$ for SO_2.

The presence of residual conductance factors that influence SO_2 but not H_2O vapor merits additional comment. The influence of residual factors was not considered in most SO_2 flux studies (e.g., Winner and Mooney, 1980a; Kimmerer and Kozlowski, 1981), even though these factors were suggested by other authors (Black and Unsworth, 1979a; Bressan et al., 1978; Hällgren, 1978; Heath, 1980). Some of the studies suggest that these residual factors

decreased the SO_2 flux below the level expected based on gas-phase (primarily stomatal) conductance (Hällgren et al., 1982). Decreased conductance associated with residual factors has been described for other pollutants, e.g., O_3 (Taylor and Tingey, 1982), and H_2S (Cope and Spedding, 1982). Other data suggest that SO_2 conductance is higher than expected from gas-phase conductance values (Klein et al., 1978; Taylor and Tingey, 1983).

Given all of the above considerations and questions concerning methodology, very few studies appear to provide a critical investigation of variability in gas-phase flux within species. Additional studies are required with necessary experimental controls to be able to accurately calculate surface loss and residual conductance to insure the same $J_{internal}$ for subsequent research concerning variability in perturbation, homeostasis, and injury within species.

Variability in boundary layer conductance and $J_{surface}$. Available data suggest that $J_{surface}$ may vary within some species but not others (Table 2); however, it has actually been measured in only a few studies (Elkiey and Ormrod, 1980b, 1981b; Taylor and Tingey, 1981). Elkiey and Ormrod reported variability in $J_{surface}$ for SO_2 in Petunia hybrida (1980b) and Poa pratensis (1981b) cultivars, but it was correlated with leaf injury only in Petunia hybrida (Table 3). The most SO_2-tolerant Petunia hybrida cultivar, 'Capri,' exhibited the highest $J_{surface}$ and had the roughest cuticule and largest number of trichomes (Elkiey et al., 1979). These cuticular characteristics could decrease boundary layer conductance which, in combination with SO_2 removal by the leaf surface, would lead to a lower SO_2 concentration at the stomatal pore reducing $J_{internal}$ compared to the other cultivars. A potential problem with Elkiey and Ormrod's studies was the lack of information concerning how the chamber sorption for SO_2 was measured. If chamber sorption was

not determined at the same dewpoint as when plants were present, SO_2 loss to the chamber system would have been underestimated producing errors in $J_{surface}$ and $J_{internal}$. A more serious potential problem would have occurred if stomatal closure in the dark had not been checked by porometry and stomatal impressions. If conductance varied in the dark, then the estimations of $J_{surface}$ would have been inaccurate and $J_{internal}$ could not have been reliably estimated (Elkiey et al., 1982).

Resistant populations of Geranium carolinianum had a slightly higher $J_{surface}$ than sensitive populations (Table 3) with the difference increasing with the SO_2 concentration (Taylor and Tingey, 1981). However, in this study, $J_{surface}$ values were not correlated with SO_2 resistance as $J_{internal}$ was similar for both populations. For the studies with Geranium carolinianum, the sorptive losses of SO_2 to the chamber were determined at the same dewpoint as when the plants were present. In addition, the leaf conductance (combination of boundary layer and stomatal conductance) values in the dark were low indicating that the stomata for both populations were probably closed (Taylor and Tingey, 1981).

Morphological data also suggest variability in $J_{surface}$ among selections of SO_2-tolerant vs. sensitive plants. In Picea abies, needles from resistant clones were longer and wider than needles from sensitive clones (Braun, 1977b). Euphorbia pulcherrima leaves from resistant cultivars had a greater trichome density than leaves from sensitive cultivars (Krizek et al., 1982). However, since $J_{surface}$ was not measured in either species, it is uncertain whether these features actually influenced SO_2 uptake. Furthermore, in both species additional factors also appeared to influence SO_2 resistance (Braun, 1977a; Krizek et al., 1982).

Variability in stomatal conductance. Many studies have focused on stomatal conductance, morphology, or density as the principal factor controlling differential SO_2 injury among plant selections (Table 2) because the stomata are the principal pathway by which gases diffuse into the leaf. In the majority of these studies, it was assumed that stomatal conductance to H_2O vapor was proportional to $J_{internal}$ for SO_2. Differences in stomatal conductance were observed in many species, both as a specific response to SO_2 exposure and as a pre-existing condition which may determine the variation in injury within species. Resistant cultivars of Glycine max (Amundson and Weinstein, 1981) and Pelargonium spp. (Bonte et al., 1977) exhibited greater stomatal closure than sensitive ones in response to SO_2 exposures, suggesting a reduction in $J_{internal}$ for SO_2. For both species all cultivars showed similar conductance in SO_2-free air. Resistant clones of Picea abies exhibited enhanced stomatal closure during SO_2 exposures and also had a lower stomatal conductance in SO_2-free air compared to sensitive clones (Braun, 1977c).

In other species, differential plant response to SO_2 was not clearly associated with variability in stomatal conductance. Resistant populations of Dactylis glomerata, Holcus lanatus, and Lolium perenne (Ayazloo et al., 1982) all had a lower conductance in SO_2-free air when compared to sensitive populations. However, in response to an SO_2 exposure, the leaf conductance of tolerant populations of D. glomerata and H. lanatus decreased but there was no change in L. perenne. Populus tremuloides clones tolerant to SO_2 had a lower leaf conductance than sensitive clones in SO_2-free air, whereas in response to SO_2, the leaf conductance decreased in sensitive clones but did not change in tolerant ones (Kimmerer and Kozlowski, 1981). Data on the stomatal conductance of Lolium perenne clones in SO_2-free air are contradictory; Ayazloo et

al. (1982) reported a lower conductance for resistant populations while Bell and Mudd (1976) found no difference between clones. Resistant cultivars of Euphorbia pulcherrima exhibited a lower stomatal conductance than sensitive cultivars in SO_2-free air (Krizek et al., 1982).

No difference in stomatal conductance either in response to SO_2 or in SO_2-free air was observed among cultivars of other species. Both cultivars of Vitis lambrusca exhibited similar patterns of stomatal opening (Schertz et al., 1980a), whereas all cultivars of Malus domestica exhibited stomatal closure in response to SO_2 exposure (Schertz et al., 1980b). Cultivars of Petunia hybrida (Elkiey and Ormrod, 1979a) and populations of Geranium carolinianum (Taylor, 1976; Taylor and Tingey, 1981) had similar stomatal conductances in SO_2-free air, and showed little change in conductance during SO_2 exposure.

In summary, even though stomatal conductance varies within species, the importance of this variation in relation to resistance to SO_2 injury depends on the species and its interpretation is influenced by the inherent problems with the methodology as described earlier. All previous studies except possibly that of Braun (1977c) used H_2O vapor as a surrogate for SO_2, and most did not consider the effects of boundary layer conductance and residual factors on SO_2 flux.

Variability in J_{total} and $J_{internal}$. Intraspecific differences in SO_2 flux, both J_{total} and $J_{internal}$ have been compared for plant selections showing differential injury in only a few species (Table 2). Total SO_2 flux varied among populations of Cucumis sativum and Cucurbita pepo, with resistant cultivars exhibiting 40 and 13% lower J_{total}, respectively, than corresponding sensitive cultivars (Bressan et al., 1978). In Petunia hybrida, J_{total} varied 27% between cultivars (Mikkelsen et al., 1981); however, variability within

cultivars was of the same magnitude and there was no correlation between J_{total} and resistance to SO_2. This lack of correlation between J_{total} and injury, in Petunia hybrida, as reported by Mikkelsen et al. (1981) may be due to variation in $J_{surface}$ as documented by Elkiey and Ormrod (1980a). In the case of Petunia hybrida, use of different cultivars by the two research groups may also have contributed to the difference in results.

Elkiey and Ormrod found considerable intraspecific variability in $J_{internal}$ for Poa pratensis (1981b) and Petunia hybrida (1981b, 1981a) cultivars differing in foliar injury (Table 3). In Poa pratensis, $J_{internal}$ was 22% lower in three resistant cultivars compared to two sensitive cultivars. For cultivars of intermediate sensitivity, $J_{internal}$ was similar to both resistant and sensitive cultivars. In Petunia hybrida, $J_{internal}$ was approximately 30% lower in the resistant compared to sensitive cultivar. For the intermediate sensitivity cultivar, $J_{internal}$ was similar to the sensitive cultivar.

In addition to the chamber loss considerations described earlier, the data (Elkiey and Ormrod, 1980b, 1981a, b) were not evaluated for possible variability in g_a as reflected by the large differences in $J_{surface}$. Variability in g_a would decrease the SO_2 concentration at the stomatal pore, thereby reducing the SO_2 concentration gradient between the pore and leaf interior, producing a lower $J_{internal}$ than expected from the atmospheric SO_2 concentration. This concern may be especially important in Petunia hybrida, as the resistant cultivar had a much larger $J_{surface}$ than the sensitive cultivar, possibly resulting in a decrease in cuticular SO_2 concentration large enough to account for the lower $J_{internal}$ for the resistant cultivar.

Taylor and Tingey (1981) reported only a slight difference in $J_{internal}$ between two populations of Geranium carolinianum (Table 3). The resistant

population exhibited an average of 5-11% lower $J_{internal}$ than the sensitive population over a range of SO_2 concentrations, compared to a much larger (9-68%) variability in J_{total} or $J_{surface}$ within each population. For Geranium carolinianum, $J_{surface}$ was similar for both populations and the cuticular SO_2 concentration was adjusted for boundary layer conductance.

Sulfur enrichment. Gas-phase conductance can be estimated by measuring sulfur enrichment to a plant during exposure, with sulfur content evaluated as either ^{35}sulfur or as nonradioactive total sulfur or sulfate-sulfur (Table 4).

Enrichment with ^{35}sulfur did not vary between resistant and sensitive populations of Dactylis glomerata, Holcus lanatus (Ayazloo et al., 1982), or populations and clones of Lolium perenne (Garsed and Read, 1977; Ayazloo et al., 1982). For each species, similar ^{35}sulfur concentrations were washed from leaves fumigated with $^{35}SO_2$ indicating that $J_{surface}$ was similar for both resistant and sensitive plants. In addition, ^{35}sulfur concentrations in internal fractions (methanol: chloroform:H_2O + N-ethylmaleimide soluble and insoluble) indicated that ^{35}sulfur concentrations were similar. For Festuca rubra, the resistant population had 43% lower ^{35}sulfur in the leaf wash solutions compared to the sensitive population (Ayazloo et al., 1982). However, ^{35}sulfur was essentially the same in the internal fractions. These data illustrate the ^{35}sulfur uptake method (Garsed and Read, 1974, 1977) for determining $J_{surface}$ and $J_{internal}$ without the problems inherent in measuring differential SO_2 concentrations.

Nonradioactive total sulfur content of plant tissues following an SO_2 exposure has been evaluated for plant selections within a number of species. Four herbaceous plants: Lolium perenne (Bell and Mudd, 1976), Lycopersion esculentum (Howe and Woltz, 1981), Nicotiana tabacum (Miyake and Uno, 1973), and Petunia hybrida (Elkiey and Ormrod, 1981c) exhibited little variation in

total sulfur content even though plant selections within these species exhibited differences in injury or growth. Zea mays cultivars showed no differences in total sulfur content (Laurence, 1979). There was no difference in total sulfur content between resistant and sensitive clones of Picea abies (Braun, 1977d). Pinus strobus (Roberts, 1976) exhibited a higher total sulfur content in resistant than sensitive clones, while Populus tremuloids (Kimmerer and Kozlowski, 1981) exhibited a lower total sulfur content in resistant than sensitive clones following exposure to SO_2.

Total sulfur content in Populus tremuloides paralleled stomatal conductance; the lowest total sulfur content was observed in resistant clones which also had the lowest stomatal conductance (Kimmerer and Koslowski, 1981). The authors assumed that the net increase in total sulfur content with SO_2 exposure represented $J_{internal}$, and, thus concluded that SO_2 resistance in Populus tremuloides was determined by gas-phase conductance. However, the total sulfur content actually represents J_{total}. In contrast, other researchers found no correlation between total sulfur content and stomatal conductance (Biggs and Davis, 1981; Elkiey and Ormrod, 1979a, 1980b, 1981a, c). Also, the total sulfur content does not consider compartmentalization of sulfur into different fractions or translocation of sulfur to different organs of plants, factors which may be important in determining SO_2 resistance (Garsed and Read, 1974, 1977).

Sulfate-sulfur was correlated with resistance to SO_2 in Picea abies and Pinus strobus, with resistant clones exhibiting a lower sulfate-sulfur content than sensitive clones (Rohmeder et al., 1962). In Petunia hybrida, the cultivars varied in sulfate-sulfur content for plants exposed at a high relative humidity, whereas all cultivars had similar sulfate-sulfur contents when plants were exposed at a low relative humidity (Elkiey and Ormrod,

1981c). Sulfate-sulfur was not correlated with resistance to injury at either humidity level (Elkiey and Ormrod, 1979d). Sulfate-sulfur may be a more appropriate indicator of sulfur enrichment than total sulfur as sulfate is the major product of SO_2 metabolism in plant tissue (Weigl and Zeigler, 1962; DeCormis, 1969).

Liquid-phase conductance. Thomas et al. (1950) proposed that phytotoxicity resulted from the diffusion of SO_2 through the stomata into the mesophyll where toxic metabolites were formed. Injury was the consequence of SO_2 uptake surpassing detoxification reactions in the mesophyll allowing toxic metabolites to exceed cellular concentration thresholds causing a plant response. The lack of a consistent correlation between SO_2 uptake and plant response (Table 2) supports this concept that gas-phase conductance alone is not a sufficient mechanism to explain intraspecific variability in injury. Several studies have suggested that plants have "avoidance" (i.e., pollutant exclusion) and "tolerance" (i.e., control of toxicity) mechanisms that contribute to inter- and intraspecific variation in injury (Taylor, 1978b; Ayazloo et al., 1982). For example, studies on resistance to SO_2 within populations of several grass species found that there was no correlation between the degree of acute and chronic injury, suggesting independent mechanisms for tolerance (Ayazloo and Bell, 1981). Alterations in the liquid-phase conductance of SO_2 may contribute, in part, to intraspecific variability in injury.

Following the diffusion of SO_2 through the stomata, there are additional pathways for SO_2 transfer which may constitute internal hinderances to SO_2 conductance. These hinderances may include internal components of SO_2 metabolism such as solubilization in the H_2O film on the cell surface, conversion into additional compounds, and transport (Jäger and Klein, 1980).

Following dissolution into H_2O in and on the cell, SO_2 is rapidly hydrated, forming bisulfite and sulfite (Peiser and Yang, 1983). At typical cellular pH values, bisulfite is the dominant species but the proportion of sulfite increases with pH (Ziegler, 1975; Peiser and Yang, 1983). Both bisulfite and sulfite have been implicated in SO_2 toxicity with the complex being approximately 30 times more toxic than sulfate (Thomas, 1961).

Sulfite and bisulfite may be detoxified by either oxidative or reductive reactions (Fig. 3). Depending on the redox conditions prevailing within the cells, sulfite may undergo auto-oxidation or possibly oxidation by a mitochondrial sulfite oxidase (Ziegler, 1975; Hällgren, 1978). Sulfite may also be photo-oxidized to sulfate by a free radical chain process that is initiated by superoxide anion produced via the photosynthetic electron transport system in the chloroplast (Asada, 1980; Peiser et al., 1982). In addition to oxidation to sulfate, sulfite may also be photoreduced to sulfide and subsequently volatilized as H_2S (Silvius et al., 1976).

The oxidation of sulfite to sulfate has been proposed as a potential detoxification mechanism for SO_2. Variability in oxidation rate and tissue sulfite concentration has been associated with differential plant responses to SO_2. Exogenous sulfite was metabolized more rapidly in Glycine max cultivars resistant to foliar SO_2 injury than in sensitive cultivars (Miller and Xerikos, 1979). Studies with Lycopersicon esculentum plants (Howe and Woltz, 1981) showed that foliar sulfite levels increased with the SO_2 exposure concentration illustrating the association between uptake and cellular metabolic concentrations. In addition, foliar injury was highly correlated with tissue sulfite concentrations, confirming the observations of Miller and Xerikos (1979).

Kondo et al. (1980) reported that SO_2 tolerance among species was correlated with a sulfite oxidase activity. Ayazloo et al. (1982) found that a sensitive genotype of Lolium, S23, had a higher proportion of inorganic sulfur as sulfite than the tolerant genotypes following both light and dark incubations in sulfite solutions. They also reported that of the populations of several species exhibiting differential sensitivity to SO_2, only the more tolerant population of Holcus lanatus had a higher rate of sulfite oxidation following SO_2 exposure; no significant differences in sulfite oxidation rates were observed between genotypes of two other species.

The photoreduction of sulfite to sulfide may also be a detoxification mechanism. Plants exposed to SO_2 emit H_2S in the light (DeCormis, 1968; Silvius et al., 1976; Hällgren and Fredriksson, 1982). Hydrogen sulfide was detected within 15 to 30 minutes after the start of exposure with emissions reaching a maximum within 45 minutes (DeCormis, 1968; Taylor and Tingey, 1983). A $J_{internal}$ of at least 48 μmol SO_2 m^{-2} was required to stimulate emissions, suggesting that the cellular concentration had to exceed a threshold before emissions occurred (Taylor and Tingey, 1983). Dodrill (1976) suggested that the emission of H_2S was a method of detoxifying SO_2 as H_2S emissions were stimulated at lower SO_2 concentrations than require to cause foliar injury. Young leaves of Cucumis sativus plants were resistant to acute exposures of SO_2, but older leaves were sensitive even though they absorbed less SO_2 (Sekiya et al., 1982a). The authors suggested that the differential sensitivity between different-aged leaves of Cucumis sativus cultivars occurred because the young leaves possessed a higher capacity to photoreduce SO_2 to H_2S. In contrast, H_2S emissions were similar from plants of populations of Geranium carolinianum even though they differed in SO_2 sensitivity (G. Taylor, personal communication). In some species, emission of H_2S may

provide a means of detoxifying SO_2 if the sulfide is formed by the photoreduction of sulfite. In some plant systems, cysteine may also be metabolized into H_2S (Rennenberg et al., 1982; Sekiya et al., 1982b); but in this case H_2S would apparently not contribute to detoxification.

Studies on the inheritance of resistance to SO_2 injury in inbred lines and crosses of Cucumis sativus lead to the conclusion that the plasma membrane was a barrier to the uptake and transport of both SO_2 and sulfite (Bressan et al., 1981). The authors suggested that this barrier contributed to the differential sensitivies of plants to SO_2. They supported this conclusion by the observation that the relative resistance to SO_2 or bisulfite was the same for a variety of other stresses likely to affect membrane properties.

The buffer capacity of plant tissue to hydrogen ions was decreased by SO_2 exposures without an accompanying decrease in cellular pH (Thomas et al., 1950; Jäger and Klein, 1977). Although buffer capacity has been implicated in plant resistance to SO_2, the few investigations of variability in buffering capacity within species produced conflicting results. Resistant clones of Picea abies had a higher buffering capacity than sensitive clones (Scholz and Reck, 1976; Braun, 1977d). No difference in buffering capacity was found between two populations of Muhlenbergia asperifolia (Campbell, 1972).

In summary, both gas- and liquid-phase conductance pathways control SO_2 flux to cellular perturbation sites within leaves. Interspecific variation in gas-phase components: g_a, g_s, $J_{surface}$, and $J_{internal}$ occurs in a wide range of species. However, this variability was not consistently associated with differential plant injury. Considerable study remains to be done to understand gas-phase conductance of SO_2, with particular emphasis on rigorous evaluation of methodology and documentation of components indicating metabolically active SO_2, e.g., $J_{internal}$. Liquid-phase conductance presently is

poorly understood. However, recent evidence suggsets that mesophyll detoxification reactions are important in controlling plant response to SO_2, highlighting the need for critical study of components of liquid-phase conductance.

Perturbation

Perturbation, as defined here, is the initial SO_2-induced change in cell structure and/or function. Phytotoxicity results from the spontaneous reaction of bisulfite-sulfite or the free radicals produced by their oxidation with macromolecules required to maintain cellular function. Evidence from a variety of sources suggests that the primary SO_2 toxic effects occur within the chloroplasts. The initial ultrastructural changes associated with SO_2 exposures are swelling of the thylakoids without other effects being observed; swelling is reversible if the SO_2 is removed (Wellburn et al., 1972; Wong et al., 1977).

When plants are exposed to radioactive SO_2, the sulfite formed within the cytoplasm is incorporated into the chloroplasts, mitochondria, and peroxisomes. The sulfur is uniformly distributed in the protein moieties of the mitochondria and peroxisomes but in the chloroplasts there is a preferential incorporation into the thylakoid membranes (Ziegler, 1977). In the light, superoxide anion free radicals are produced on the surface of the thylakoid membranes as a result of electron transport and these free radicals initiate the chain oxidation of sulfite to sulfate (Asada and Kiso, 1973; Asada, 1980; Peiser et al., 1982). Concurrent with the free radical chain oxidation of sulfite to sulfate is the production of increased amounts of hydroxyl, bisulfite, and additional superoxide anion free radicals which are cytotoxins that can oxidize chloroplast membranes (Asada, 1980; Peiser et al., 1982).

Sulfur dioxide may also form free radicals indirectly in the chloroplast, e.g., conditions such as stomatal closure which would reduce the amount of CO_2 for photoreduction can also cause an increased superoxide anion production (Asada, 1980). Free radical disruption of chloroplast membranes also would affect electron transport which could contribute to photo-oxidative injury in the cells. This is consistent with the suggestion of Noack (1929) that SO_2 interfered with the catalytic properties of the chloroplast and induced photo-oxidative processes that promoted chlorophyll decomposition and cell death.

Several types of evidence suggest that free radical formation is involved in SO_2 phytotoxicity. Foliar applications of free radical scavengers such as α-tocopherol, diphenylamine, or propyl gallate reduced foliar injury induced by SO_2 (Chang et al., 1981). The enzyme superoxide dismutase (SOD) disproportions free radicals forming hydrogen peroxide which is metabolized by catalase to H_2O and oxygen. Low concentrations of SO_2 have been reported to induce SOD in Populus euramericana leaves imparting protection against subsequent exposures to a higher concentration (Tanaka and Sugahara, 1980). The same authors showed that a copper chelator that reduced SOD activity increased SO_2 toxicity. They also attributed the greater SO_2 tolerance of young Populus euramericana leaves compared to old ones to a higher SOD activity. Asada (1980) proposed that SOD was a tolerance mechanism for SO_2 injury because it inhibited the chain oxidation of sulfite to sulfate (Asada, 1980; Ziegler, 1975). If the SOD scavenged the superoxide anion used to initiate sulfite oxidation as suggested by Asada (1980), this would prevent the chain oxidation of sulfite and the resultant free radicals but sulfite and bisulfite, also phytotoxic, would remain. Given the increased free radical production during

oxidation of sulfite to sulfate, it is not clear that this is a reliable detoxification mechanism.

Most plants close their stomata in the dark and thus are assumed to be much more tolerant of SO_2 than in the light. However, in species where the stomata may not close (e.g., potato), the leaves are more sensitive in the dark than light (Nielsen, 1938). Individual alfalfa leaves that were observed to have open stomata in the dark displayed a similar SO_2 sensitivity as in light exposures (Thomas, 1961). The phytotoxicity observed in the dark suggests that other SO_2 metabolites such as bisulfite-sulfite were also phytotoxic in addition to photochemical-induced free radicals. Bisulfite has been shown to alter the selective permeability of plant membranes in both the light and dark (Lüttge et al., 1972) and it may disrupt disulfide bonds in proteins, altering structure and activity.

There have been no studies of within-species variability of the initial perturbation from SO_2. Limited studies, with mixed results, have been conducted on the possible effects of SO_2 on the permeability of the plasmalemma. The relationship between membrane permeability and resistance to SO_2 injury was evaluated in six species using potassium leakage or conductivity as an indicator of membrane integrity. No difference in potassium leakage was observed between cultivars of Petunia hybrida (Elkiey and Ormrod, 1979b) or clones of Picea abies (Braun, 1977b). No consistent pattern in membrane permeability was observed in sensitive and resistant populations of four grass species; resistant and sensitive populations had similar potassium leakage rates following SO_2 exposure (Ayazloo et al., 1982). The lack of consistent results in plasmalemma permeability is not surprising since the primary effects of SO_2 seem to occur within the chloroplast. Substantial metabolic

changes may occur before there are substantial changes in the outer limiting membrane.

Homeostasis

Following perturbations, living systems begin reestablishing their normal metabolic state. Recovery may be accomplished by repair and/or compensation of the perturbation and its consequences (Levitt, 1972). Although the final state (i.e., recovery) from each process is similar, the underlying mechanism(s) differ(s) for each. The repair processes rectify the perturbation thereby eliminating its physiological dysfunction. Compensation is somewhat different from repair in that the perturbation and its physiological consequences persist. However, in the case the cell responds with processes that counter the detrimental effects of the perturbation. Because the repair or compensation of the cellular perturbation may range from partial to complete, the plant response will vary to a similar extent.

There have been very few studies on homeostatic processes in plants following SO_2 exposure; however, such responses would be expected to occur just as they do for other pollutants such as O_3. Repair of O_3 injury involves the reestablishment of normal membrane processes and apparently is an active process requiring energy. Differential plant sensitivity to ozone has been attributed to differences in endogenous repair rates (Taylor and Tingey, 1982).

One of the early visual symptoms of acute SO_2 injury is the appearance of H_2O-soaked interveinal areas on leaves. If these areas are not subjected to extensive drying by either wind or sunshine, the H_2O may be reabsorbed into the cells resulting in little or no visual injury (Thomas et al., 1950), indicating that the initial stages of injury are reversible. Wellburn et al.

(1972) reported that the SO_2-induced swelling of thylakoids was reversible if the pollutant was followed by clean air. This response also suggests that homeostatic processes were operative.

The SO_2-induced depression of photosynthesis (e.g., Winner and Mooney, 1980a, b; Black and Unsworth, 1979b; Bennett and Hill, 1973) is a commonly observed response (Table 5), and probably results from the disruption of the chloroplast membranes. When SO_2 is removed, the photosynthetic rate rapidly returns to the pre-fumigation level unless acute injury has occurred (e.g., Black and Unsworth, 1979b; Bennett and Hill, 1973). This recovery is probably a consequence of homeostatic processes repairing the altered chloroplast membranes, unless the depressed photosynthesis was a result of only a decreased leaf conductance to CO_2. The recovery from the SO_2-induced depression of photosynthesis may provide a mechanism to investigate homeostatic processes.

Chronic SO_2 exposures can increase the polyamine content of pea plants (Priebe et al., 1978). These authors suggested that one of the important metabolic functions of polyamines was the regulation of cellular pH because the polyamines can function as polyvalent cations. Thus, the relative cation deficiency induced by SO_2 exposures may be partially compensated for by the synthesis of polyamines (Priebe et al., 1978). Polyamines have also been reported to stabilize cellular membranes (Naik and Srivastava, 1978) which may serve to protect membrane integrity in the presence of SO_2.

In C_3 plants, photorespiration may be a mechanism of preventing the electron transport chain, in the chloroplasts, from being oxidized and increasing free radical formation. From this perspective, photorespiration may also contribute to homeostatic processes in plants.

The repair and/or compensatory processes that are induced by SO_2 perturbation are areas needing additional research. As studies are conducted they should consider the probable initial effects of SO_2. In addition, the physiological responses measured should assess the rate of repair. There also may be different homeostatic processes for acute and chronic perturbations.

Injury

Injury is the result of perturbations that are not repaired or compensated. Because the initial SO_2-induced perturbations apparently occur at selected sites within the cell such as the chloroplast, the initial metabolic dysfunctions probably originate in specific organelles or cellular regions. Biochemically, injury consists of changes in metabolism including effects on enzyme activities and metabolite pools. The altered biochemical processes when summed across numerous cells are expressed as altered tissue and organ activities, which in turn may induce foliar injury symptoms, altered carbon allocation and changes in plant growth, reproduction, and yield. These changes are all consequences of the SO_2 perturbation rather than the initial perturbation itself. The magnitude of the plant response or injury observed reflects the extent to which homeostatic processes are unable to correct the perturbation.

Intraspecific variation in plant response to SO_2 has been reported for effects ranging from changes in enzyme activities and metabolite pools to changes in plant pigments (Table 5). Many of the responses such as altered photosynthesis, changes in plant pigments, and altered enzyme activities are typical stress responses that have been also observed with other air pollutants and various abiotic and biotic stresses. They represent the consequences of altered cellular function but are not the cause of the perturbation. As

our knowledge of homeostatic processes improve, certain of these metabolic changes may in fact be associated with repair or compensatory processes correcting secondary or tertiary perturbations resulting from the initial SO_2 effect. For example, the reduction in photosynthesis (e.g., Börtitz and Vogl, 1965; Grzesiak, 1979; Lorenc-Plucinska, 1982) is a transient response unless there is extensive tissue injury. This reduction is a consequence of, but is probably not the primary SO_2 perturbation. The restoration of normal metabolic activity following SO_2 exposure results from the repair of altered membrane function or enzyme activities necessary for the process, and illustrates the probable occurrence of homeostatic processes for these secondary perturbations.

Plants exposed to SO_2 have been shown to emit both ethylene and ethane (Peiser and Yang, 1979; Bressan et al., 1979). Ethylene emissions began shortly after exposure, peaked within 1 to 8 hr, and were produced in greater quantity in the dark than in light (Peiser and Yang, 1979). Ethane emissions were associated with visual injury and production was stimulated by light (Peiser and Yang, 1979). The release of ethylene is a general stress response that is elicited by air pollutants and numerous other stresses. In contrast, ethane emissions were not stimulated by O_3, various metals, or organic compounds that induced ethylene production, and emissions were similar in the light and dark (Tingey, unpublished data). Ethane is apparently formed by lipid peroxidation (Peiser et al., 1982) initiated by free radicals formed during the aerobic oxidation of sulfite to sulfate. The lipid peroxidation may be associated with, or a consequence of, the initial SO_2 perturbation (Shuwen et al., 1981; Peiser et al., 1982). However, it is not clear if the lipid peroxidation is closely associated with the initial perturbation because it takes several hours after exposure for emissions to increase. In either

case, the emission of ethane as an indicator of lipid peroxidation may be a useful indicator of perturbation provided the limitations of the data are considered.

Based on the multiplicity of physiological mechanisms responsible for variable plant responses to SO_2, a common progression of events is proposed beginning with SO_2 conductance (gas and liquid phase), continuing through perturbation and homeostasis, finally terminating with injury. Injury is the consequence of the preceding events. Numerous studies have attempted to document the significance of gas-phase conductance; far fewer studies have been conducted on liquid-phase conductance issues. The importance of perturbation and homeostasis has not been well documented.

The association between gas-phase conductance and injury has been equivocal. From the conceptual model, it is obvious that gas-phase conductance would be the decisive factor controlling plant response only if it were the limiting factor. Physiologically significant processes that occur between gas-phase conductance and injury would decrease the association. Because plant response is not always correlated with gas-phase conductance (i.e., SO_2 uptake), it is self-evident that liquid-phase conductance and homeostasis are important factors influencing SO_2 response.

Importance of Metabolic Variability

Metabolic variability within species is an important tool for both understanding the mechanism of plant response to SO_2, and as a basis of screening plant populations for individuals that may exhibit resistance to SO_2 for use in genetic studies. Ideally, a physiologic parameter that achieves both objectives would be most useful. However, in practice, certain physiological parameters may be more appropriate as indicators of the mechanism for

resistance, whereas other parameters may provide information for genetic studies.

The source of variation in foliar injury among plants to SO_2 is not clear. Only a few reports are available describing variation within species for SO_2 flux into leaves. In studying plant responses to SO_2, it is important to know the internal exposure as SO_2 exerts its metabolic effects within the leaf. This exposure must be defined and quantified to understand plant response, as it is the dose reaching the perturbation sites and not the ambient concentration that is important. Only when studies have assured that the internal exposures are similar between treatments of a plant selection is it possible to accurately interpret plant response data. In studies on the perturbation mechanism, it has not been possible to determine if the variable responses reflect differences in the sensitivity of the particular site between plant selections or only the fact that different amounts of SO_2 reached the active site. The same problem complicates the interpretation of homeostatic processes and metabolic changes associated with injury. Differentially sensitive strains within species should provide a useful means for studying the perturbation mechanism if equality of cellular exposure is assured. The metabolic variability should be smaller within than between species, making it easier to detect changes in metabolites that may be related to sensitivity.

Only a few studies have attempted to study a broad range of responses that may contribute to differential sensitivity on the same species (e.g, Ayazloo et al., 1982; Braun, 1977a; Elkiey and Ormrod, 1979a, b, c, 1980b, 1981c). Such comprehensive studies should be encouraged. Only by considering a range of responses on a few plant selections and understanding the influence

of cellular exposures will we be able to make progress in understanding the causes of plant response to SO_2.

For genetic studies, parameters which indicate plant injury, e.g., chlorophyll content (Schindlbeck, 1977), peroxidase activity (Wellburn et al., 1976), ethane emissions (Bressan et al., 1979), or visible necrosis as in the German "Rapid Test" for trees (Börtitz and Vogl, 1965), may be used to evaluate the resistance of parent or progeny plants to SO_2. The parameter chosen should support the research aims and allow the quantitative screening of a large number of plants within a short time period.

Other parameters more directly linked to a mechanism for resistance to injury, such as internal SO_2 flux (Elkiey and Ormrod, 1981a; Taylor and Tingey, 1981), or sulfite metabolism (Howe and Woltz, 1981; Miller and Xerikos, 1979; Asada, 1980), may be effective indicators of plant response once the resistance to SO_2 has been established in various lines. Individual plants with these characteristics could then be used for further study to produce tolerant progeny. If possible, the parameter should be related physiologically to plant productivity, e.g., stomatal conductance influences pollutant flux and thereby the photosynthetic rate and hence yield. Characteristics not necessarily associated with either injury or physiology of resistance, such as isoenzyme patterns (Mejnartowicz et al., 1978), may not be appropriate for breeding research.

Prospects and procedures for breeding plants resistant to SO_2 have been described for agricultural crops (Ryder, 1973; Guderian, 1977) and trees (Demeritt et al., 1972; Jensen et al., 1976; Bialobok, 1979, 1980; Scholz, 1981). Breeding progress in some species, e.g., Larix spp., has occurred to the extent that resistant strains are available for forest testing (Enderline et al., 1967). The particular methods used in breeding of course depend on

the species in question; but, in general, the process of producing plants resistant to SO_2 would be expected to be similar to the process of developing plants with disease resistance or other desirable characteristics.

The obvious differences in SO_2 sensitivity within species (Table 1) illustrate the heritability of SO_2 resistance which has been documented by studies such as the clonal repeatability tests for Pinus strobus (Houston and Stairs, 1973) and Populus tremuloides (Karnosky, 1977). However, the genetic system for resistance to SO_2 has been evaluated in only a limited number of species. Additive inheritance was found in Geranium carolinianum (Taylor, 1978a) which was not associated with leaf conductance parameters. In contrast, one or two genes appeared to control SO_2 resistance in Cucumis sativus (Bressan et al., 1981) and Oryza sativa (Omura et al., 1980), indicating that a relatively simple physiological mechanism controlled injury. Studies of SO_2 flux and bisulfite sensitivity in Cucumis sativus selections indicated that, while SO_2 flux was lower in the resistant than sensitive selections, injury was not necessarily dependent on stomatal conductance (Bressan et al., 1978, 1981). General inheritance was demonstrated when parents and progeny of Pinus sylvestris (Vogl, 1970) and Larix spp. (Enderline et al., 1967) were examined for SO_2 resistance; however, in these studies the mechanism was not evaluated. Based on this limited research, the genetic systems for resistance to SO_2 appear to parallel those for O_3 where resistance is controlled by few to many genes (Butler et al., 1979; Hanson et al., 1976), indicating that the link between the nature of metabolic variability between genetic lines and the apparent system of heritability in a species could provide a profitable area of research.

Direct genetic and reproductive effects of SO_2 (Shapiro, 1977) could have a significant impact on breeding for resistance. SO_2 decreased pollen

germination and tube growth in Pinus strobus (Karnosky and Stairs, 1975) and Tradescantia paludasa (Ma and Khan, 1972); SO_2-enhanced chromosome aberrations also were found in Tradescantia paludasa pollen tube cultures (Ma et al., 1973). Reduced seed production and abortion of seeds was reported in conifers injured by ambient SO_2 (Hedgecock, 1912; Mamajev and Shkarlet, 1970).

Variation in reproductive response to SO_2 within species could be important both in breeding programs and in natural environments. Research by Murdy (1979) on Lepidium virginicum indicated that greater fertility in polluted environments was associated with resistance of populations to SO_2. Examination of the metabolic basis for this or other reproductive responses in other species would be a significant contribution to an understanding of the long term effects of SO_2 on plant populations.

The potential of selecting for SO_2 resistance is evident from the evolution of resistant populations of plants growing in areas subjected to SO_2 emissions over a long period of time (Bradshaw, 1976; Taylor and Murdy, 1975; Roose et al., 1982). In these cases, resistance was documented by comparing the response of populations from affected and non-affected areas when both groups were exposed to SO_2 under controlled laboratory conditions. For three pasture grasses, Dactylis glomerata, Festuca rubra, and Holcus lanatus, resistance was observed in terms of both reduced leaf injury and enhanced growth (Ayazloo and Bell, 1981), In Lolium perenne (Ayazloo and Bell, 1981), resistance was indicated by enhanced growth but no difference in injury was found between the two populations. Resistance in Geranium carolinianum was evaluated only in terms of reduced visible injury (Taylor and Murdy, 1975), whereas in Lepidium virginicum resistance was evident as greater fertility (Murdy, 1979).

Similar cases of the evolution of resistance to pollutants has been shown in species affected by heavy metals (Antonovics et al., 1971; Wu et al., 1975), and possibly by oxidants (Dunn, 1959) and acid rain (Hodgkin and Briggs, 1981). Indeed, in areas where pollutants are a significant environmental factors, it is not surprising that over a period of time genetic mechanisms produce resistant populations (Roose et al., 1982) so that a species may adapt either by avoiding or tolerating the stress (Taylor, 1978b). Additional examples of evolution of resistance to SO_2 may be expected, especially if herbaceous species with a short generation time are evaluated (Roose et al., 1982).

If breeding for resistance to SO_2 is to become successful the general adaptability of the resistant material to the environment in which the plants are to be grown must be considered. Recent evidence indicates a complex interaction between environment and SO_2 exposure. Studies have shown that low levels of SO_2 may sensitize plants to cold injury (Huttunen, 1978; Huttunen et al., 1981; Keller, 1981; Baker et al., 1982; Davison and Bailey, 1982), possibly by increasing H_2O stress (Huttunen et al., 1981). Conversely, environmental factors may increase the SO_2 sensitivity of plants (Guderian, 1977), as shown by the increase in SO_2 injury with desiccation (Okoloko and Brewley, 1982). Thus, even if clones or cultivars are developed which are relatively resistant to SO_2, injury may occur if they are not fully adapted to their growing environment (Huttunen, 1978; Guderian and Küppers, 1980; Huttunen et al., 1981).

Summary

Variation in metabolic responses to SO_2 is widespread within many plant species. Plant responses are a consequence of a series of biochemical and

physiological events beginning with SO_2 flux into plant and progressing through perturbation, and homeostasis, and ending with foliar injury and/or effects on growth and yield. Gas-phase and liquid-phase conductance are important determinants of SO_2 flux. However, the relationship between variation in these factors and plant response is incompletely understood -- at least in part because of difficulties with SO_2 gas-exchange methodology. Perturbation events occurring primarily in the chloroplast, and homeostatic mechanisms have received only brief attention.

The entire sequence of plant response to SO_2 needs additional investigation especially to identify components useful in genetic studies of SO_2 resistance. Evidence to date demonstrates the heritability of SO_2 resistance in both native and cultivated vegetation. Understanding the mechanism for variability in plant response would improve success of breeding for resistance to SO_2 injury.

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Table 1

Intraspecific Variation in Foliar Injury Response to Sulfur Dioxide

Species	Conc.[a] (nmol l^{-1})	Time[b]	Comparison[c]	Results[d]	Reference
Agronomic Crops					
Glycine max (soybean)	83	1.75 h	19 cv	d**	Miller et al., 1974
	83	4 h	3 cv	d	Amundson and Weinstein, 1981
Hordeum vulgare (barley)	62	1 h	2 cv	nd	Baba and Sakai, 1976
Humulus lupulus (hops)	8-17	4 h (4 h d^{-1})	4 cv	d	Fiala, 1966
Medicago sativa (alfalfa)	56	4 h	5 cv	nd*	Tibbitts et al., 1982
Nicotiana tabacum (tobacco)	83	1 h	4 cv	d	Hsieh, 1973
	62	3 h	6 cv	d	Menser et al., 1973
	6, 12	50-57 d	2 cv	d	Miyake and Uno, 1973
Oryza sativa (rice)	21-83	1.5-7.5 h	303 cv	d	Omura et al., 1978
	25-29	5 h (1 h d^{-1})	22 cv	d	Valenzona et al., 1978
	83	6, 8, 12 h	4, 5 cv	d	Omura et al., 1980
Triticum aestivum (wheat)	8-25	30-100 h	4 cv	d	Laurence, 1979
Zea mays (maize)	4-21	6-100 h	7 cv	nd	Laurence, 1979
	21	20 d (5 h d^{-1})	7 lines, 2 cv	nd	Grzesiak, 1979
Grasses and Native Herbaceous Plants					
Dactylis glomerata (orchard grass)	83	6 h	2 pop	d***	Ayazloo and Bell, 1981
Festuca rubra (red fescue)	31-75	6 h	2 cv	d	Brennan and Halisky, 1970
	6	10 d (6 h d^{-1})	2 cv	d	Elkiey and Ormrod, 1980a
	82	6 h	2 pop	d	Ayazloo and Bell, 1981
Geranium carolinianum (wild geranium)	33	12 h	6 pop	d	Taylor and Murdy, 1975
Holcus lanatus (velvet grass)	83	6 h	2 pop	d**	Ayazloo and Bell, 1981
Lolium perenne (perennial ryegrass)	31-75	6 h	2 cv	d	Brennan and Halisky, 1970
	83	6 h	2 pop	nd	Ayazloo and Bell, 1981
Muhlenbergia asperifolia	41-456	8 h	2 pop	nd	Campbell, 1972
Poa pratensis (Kentucky bluegrass)	31-75	6 h	2 cv	d	Brennan and Halisky, 1970
	8	2 h	17 cv	d*	Murray et al., 1975
	6	10 d (6 h d^{-1})	12 cv	d**	Elkiey and Ormrod, 1980a
Zoysia japonica (Japanese lawngrass)	31-75	6 h	2 cv	nd	Brennan and Halisky, 1970
Horticultural Crops					
Antirrhinum majus (snapdragon)	166	2 h	3 cv	nd	Adedipe et al., 1973
Begonia x hiemalis (Eliatior begonia)	21	4 d (4 h d^{-1})	5 cv	d	Reinert and Nelson, 1980
B. semperflorens (begonia)	17-91	3, 4 h	6, 16 cv	d	Leone and Brennan, 1972
	166	2 h	3 cv	nd	Adedipe et al., 1973
Crysanthemum morifolium (chrysanthenum)	104, 187	3, 4 h	16 cv	d	Brennan and Leone, 1972
Coleus spp. (coleus)	4-124	4 h	15 cv	d*	Semeniuk and Heggestad, 1981
Cucumus sativus (cucumber)	17-37	6-24 h	2 cv	d	Bressan et al., 1978
Cucurbita pepo (squash, pumpkin)	17-37	6-24 h	2 cv	d	Bressan et al., 1978
Daucus carota (carrot)	10-36	2 h	4 cv	nd	Tibbitts et al., 1982
Euphorbia pulcherrima (poinsettia)	4-124	1-3 h	8 cv	d**	Heggestad et al., 1973
Fragaria x ananassa (strawberry)	4-42	4 d (6 h d^{-1})	6 cv	nd	Rajput et al., 1977
Hibiscus syriacus (hibiscus)	124, 2073	1 h	2 cv	d	Ahn and Yeam, 1977
Ilex aquifolium (English holly)	~29-166	6 d (7 h d^{-1})	2 cv	nd	Brennan and Leone, 1970
Lycopersicon esculentum (tomato)	41, 83	2, 4 h	26 cv	d*	Howe and Woltz, 1982a
Malus domestica (apple)	17, 83	4 h	3 cv	d**	Schertz et al., 1980b
Pelargonium spp. (cultivated geranium)	456	1 h	11 cv	d	Bonte et al., 1977

(continued)

Table 1 (continued)

Species	Conc.[a] (nmol l^{-1})	Time[b]	Comparison[c]	Results[d]	Reference
Petunia hybrida (petunia)	104, 207, 415	1 h	14 cv	d	Feder et al., 1969
	166	2 h	4 cv	d	Adedipe et al., 1973
	33	4 d (4 h d^{-1})	3 cv	d	Elkiey and Ormrod, 1979d
	116	16 h	5 cv	d*	Mikkelsen et al., 1981
Phaseolus vulgaris (bean)	42	5 d (6 h)	32 cv	d	Beckerson et al., 1979
Rhododendron spp. (azalea)	124	1-3 d (3-6 h d^{-1})	19 cv	d	Kunishige and Hirata, 1975
	10	6 h (3 h d^{-1})	8 cv	nd	Sanders and Reinert, 1982
Tagetes spp. (marigold)	42, 83	2, 4 h	39 cv	d*	Howe and Woltz, 1982b
T. patula (marigold)	166	2 h	2 cv	nd	Adedipe et al., 1973
Vitis labrusca (grapevines)	3-11	seasonal	6 cv	d	Fujiwara, 1970
	17, 33	4 h	2 cv	d**	Schertz et al., 1980a
		Trees			
Acer plantanoides (Norway maple)	42	7.5 h	8 cv	d	Karnosky, 1981
A. rubrum (red maple)	42	7.5 h	4 cv	d	Karnosky, 1981
A. saccharum (sugar maple)	42	7.5 h	3 cv	nd	Karnosky, 1981
Fraximus americana (white ash)	42	7.5 h	10 pr, 50 hsf	d**	Karnosky and Steiner, 1981
F. pennsylvanica (green ash)	42	7.5 h	2 cv	d	Karnosky, 1981
	42	7.5 h	16 pr, 59 hsf	d**	Karnosky and Steiner, 1981
Ginkgo biloba (ginkgo)	42	7.5 h	4 cv	d	Karnosky, 1981
Gleditsia tricanthos inermis (thornless honeylocust)	42	7.5	6 cv	d	Karnosky, 1981
Larix spp. (larch)	14-30	20-50 h	12 cl	d	Schönbach et al., 1964
	829	10 x (12 mx^{-1})	18 cl	d	Böritz and Vogl, 1965
	30	20-50 h	54 cl	d	Enderline et al., 1966, 1967
Picea abies (Norway spruce)	8-207	6-14 d (12 h d^{-1})	26 cl	d	Rohmeder et al., 1962
	8-33	10-28 d	36 cl	d	Rohmeder and Schönborn, 1965, 1967
	field	field	8 cl	d	Fer et al., 1972
Pinus contorta (lodgepole pine)	829	10 x (12 mx^{-1})	19 pr	d**	Tzschachsch et al., 1969
	58-66	109 h	4 pr	d**	Lang et al., 1971
	field	field	14 pr	d	Tzschacksch, 1972
Pinus strobus (eastern white pine)	4	20-40 d (4-8 h d^{-1})	2 cl	d	Dochinger and Seliskar, 1970
	1-19	6 h	30 cl	d	Houston, 1970
	field	field	600 seedlings	d	Berry, 1973
	1	6 h	10 cl	d	Houston and Stairs, 1973
	37-83	6 h	8 cl	d	Genys and Heggestad, 1978
P. sylvestris (Scotch pine)	8-207	6-14 d (12 h d^{-1})	17 cl	d	Rohmeder et al., 1962
	83	6 h	5 pr	d	Genys and Heggestad, 1978
	42-83	---	23 cl, 4 seed	d**	Mejnartowicz et al., 1978
	42-83	24 h	17 cl	d**	Smith and Davis, 1978
	83	2 h	3 sel	d*	Bialobok et al., 1980
Plantanus occidentalis (American sycamore)	83	3 h	3 pr	d	Santamour, 1969
P. orientalis	83	3 h	4 pr	d	Santamour, 1969
Populus spp. (poplar)	field	field	22 cv	d	Lampadius et al., 1970
	17-124	2 h	9 cv	d	
	166	3-12 h	4 cl	d	Dochinger et al., 1972
	10	3 d (8 h d^{-1})	2 cl	d	Dochinger and Jensen, 1975
	207	1.5-6 h	2 cl	d	Dochinger and Jensen, 1975
P. tremuloides (quaking aspen)	15-27	3 h	5 cl	d	Karnosky, 1976
	21	3 h	10 cl	d**	Karnosky, 1977
Ulmus americana (American elm)	83	3 h	4 pr	d	Santamour, 1969

(continued)

Table 1 (continued)

Species	Conc.[a] (nmol l^{-1})	Time[b]	Comparison[c]	Results[d]	Reference

[a] Concentration x 0.02413 = ppm.

[b] Abbreviations: h (hour), d (day), m (minutes), x (times).

[c] Abbreviations: cl (clone), cv (cultivar), hsf (half-sib families), pop (populations), pr (provenances), seed (seed sources), sel (selections).

[d] Abbreviations: d (difference between comparisons), nd (no difference between comparisons), ***, **, and * (statistical significance at 0.1, 1, and 5% levels, respectively), no indication (no statistical test reported).

Table 2

Intraspecific Variation in Gas-Phase Conductance

Species	Comparison[a]	Parameter[b]	Reference
No Correlation with Plant Resistance			
Cucumis sativus (cucumber)	2 cv	Stom. density	Bressan et al., 1978
Dactylis glomerata (orchard grass)	2 pop	Stom. density, length Stom. cond. SO_2	Ayazloo et al., 1982
Geranium carolinianum (wild geranium)	2 pop	Stom. cond. SO_2	Taylor, 1976; Taylor and Tingey, 1981
		SO_2 $J_{surface}$ SO_2 $J_{internal}$	Taylor and Tingey, 1981
Glycine max (soybean)	3 cv	Stom. cond. air	Amundson and Weinstein, 1981
Holcus lanatus (velvet grass)	2 pop	Stom. density, length Stom. cond. SO_2	Ayazloo et al., 1982
Lolium perenne (perennial ryegrass)	2 pop, 2 cl	Stom. density, length Stom. cond. SO_2	Bell and Mudd, 1976; Ayazloo et al., 1982
		Stom. cond. air	Bell and Mudd, 1976
Malus domestica (apple)	3 cv	Stom. cond. air Stom. cond. SO_2	Schertz et al., 1980b
Nicotiana tabacum (tobacco)	6 cv	Stom. density, width air	Menser et al., 1973
Pelargonium spp. (cultivated geranium)	11 cv	Stom. density Stom. dimensions air	Bonte et al., 1977
	2 cv	Stom. cond. air	
Petunia hybrida (petunia)	3 cv	Stom. cond. air Stom. cond. SO_2	Elkiey et al., 1979 Elkiey and Ormrod, 1979a
	5 cv	SO_2 J_{total}	Mikkelsen et al., 1981
Poa pratensis (Kentucky bluegrass)	9 cv	SO_2 $J_{surface}$	Elkiey and Ormrod, 1981b
Populus tremuloides (quaking aspen)	5 cv	Stom. cond. SO_2	Kimmerer and Kozlowski, 1981
Vitis lambrusca (grape)	2 cv	Stom. cond. air Stom. cond. SO_2	Schertz et al., 1980a
Correlation with Plant Resistance			
Cucumis sativus (cucumber)	2 cv	SO_2 J_{total}	Bressan et al., 1978
Cucurbita pepo (squash, pumpkin)	2 cv	Stom. density SO_2 J_{total}	Bressan et al., 1978
Dactylis glomerata (orchard grass)	2 pop	Stom. cond. air	Ayazloo et al., 1982
Euphorbia pulcherrima (poinsettia)	5 cv	Leaf surface Stom. cond. air	Krizek et al., 1982
Glycine max (soybean)	3 cv	Stom. cond. SO_2	Amundson and Weinstein, 1981
Holcus lanatus (velvet grass)	2 pop	Stom. cond. air	Ayazloo et al., 1982
Lolium perenne (perennial ryegrass)	2 pop	Stom. cond. air	Ayazloo et al., 1982
Pelargonium spp. (cultivated geranium)	2 cv	Stom. cond. SO_2	Bonte et al., 1977
Petunia hybrida (petunia)	3 cv	SO_2 $J_{surface}$ SO_2 $J_{internal}$	Elkiey and Ormrod, 1980b Elkiey and Ormrod, 1980b, 1981a
Picea abies (Norway spruce)	30 cl	Leaf surface morphology needle morphology gas permeability	Elkiey et al., 1979 Braun, 1977b
		Stom. cond. SO_2	Braun, 1977b; 1977c
		Stom. cond. air	Braun, 1977b
Poa pratensis (Kentucky bluegrass)	9 cv	SO_2 $J_{internal}$	Elkiey and Ormrod, 1981b
Populus tremuloides (quaking aspen)	5 cv	Stom. cond. air	Kimmerer and Kozlowski, 1981

[a] Abbreviations: cl (clones), cv (cultivars), pop (populations).

[b] Abbreviations: Stom. (Stomatal), cond. (conductance), air (no SO_2), SO_2 (during exposure to SO_2).

Table 3

Intraspecific Variability in Rates of Sulfur Dioxide Flux

Species	Cultivar	Sensitivity	Exposure (nmol ℓ^{-1}-h)	$J_{surface}$ (nmol m^{-2} s^{-1})	$J_{internal}$ (nmol m^{-2} s^{-1})
Geranium carolinianum (wild geranium)[a]	(population)	Resistant	25-0.4 h	67.3	72.9
	(population)	Sensitive		66.1	81.6
Petunia hybrida (petunia)[b]	Capri	Resistant	33-0.75 h	10.1	7.5
	White Magic	Intermediate		7.9	9.7
	White Cascade	Sensitive		1.1	9.6
Poa pratensis (Kentucky bluegrass)[c]	Fylking	Resistant	17-4 h	4.9	7.8
	Touchdown	Resistant		5.9	9.3
	Plush	Resistant		4.5	7.9
	Merion	Intermediate		8.1	8.1
	Skofti	Intermediate		6.6	11.1
	Cheri	Sensitive		9.3	10.0
	Baron	Sensitive		4.6	10.2

[a] Adapted from Taylor and Tingey (1981).

[b] Adapted from Elkiey and Ormrod (1980b).

[c] Adapted from Elkiey and Ormrod (1981a,b) using data only for day 1 from cultivars where SO_2 sensitivity was indicated.

Table 4

Intraspecific Variation in Sulfur Enrichment

Species	Comparison	Method	Reference
	No Correlation with Resistance		
Dactylis glomerata (orchard grass)	2 populations	^{35}sulfur	Ayazloo et al., 1982
Festuca rubra (red fescue)	2 populations	^{35}sulfur	Ayazloo et al., 1982
Holcus lanatus (velvet grass)	2 populations	^{35}sulfur	Ayazloo et al., 1982
Lolium perenne (perennial ryegrass)	2 clones	^{35}sulfur	Garsed and Read, 1977
	2 populations	^{35}sulfur	Ayazloo et al., 1982
	2 clones	total sulfur	Bell and Mudd, 1976
Lycopersicon esculentum (tomato)	10 cultivars	total sulfur	Howe and Woltz, 1981
Muhlenbergia asperifolia	2 populations	total sulfur	Campbell, 1972
Nicotiana tabacum (tobacco)	2 cultivars	total sulfur	Miyake and Uno, 1973
Petunia hybrida (petunia)	3 cultivars	total sulfur	Elkiey and Ormrod, 1981c
Picea abies (Norway spruce)	18 clones	total sulfur	Braun, 1977b
Zea mays (maize)	3 cultivars	total sulfur	Laurence, 1979
	Correlation with Resistance		
Petunia hybrida (petunia)	3 cultivars	sulfate-sulfur	Elkiey and Ormrod, 1981c
Picea abies (Norway spruce)	resistant vs. sensitive	sulfate-sulfur	Rohmeder et al., 1962
Pinus strobus (eastern white pine)	2 clones	total sulfur	Roberts, 1976
P. sylvestris (Scotch pine)	resistant vs. sensitive	sulfate-sulfur	Rohmeder et al., 1962
Populus tremuloides (quaking aspen)	5 clones	total sulfur	Kimmerer and Kozlowski, 1981

Table 5

Intraspecific Variation in Parameters Indicating Sulfur Dioxide Injury

Species	Comparison[a]	Parameter	Resistance Correlation	Reference
Carbon Dioxide Exchange				
Dactylis glomerata (orchard grass)	2 pop	photosynthesis	yes	Ayazloo et al., 1982
Festuca rubra (red fescue)	2 pop	photosynthesis	yes	Ayazloo et al., 1982
Holcus lanatus (velvet grass)	2 pop	photosynthesis	yes	Ayazloo et al., 1982
Hordeum vulgare (barley)	16 cv	photosynthesis	---	Brough et al., 1975
Lolium perenne (perennial ryegrass)	2 pop, 3 cl	photosynthesis	yes	Ayazloo et al., 1982
Muhlenbergia asperifolia	2 pop	photosynthesis	yes	Campbell, 1972
Picea abies (Norway spruce)	resistant vs. sensitive	photosynthesis	yes	Pelz, 1962
Pinus strobus (eastern white pine)	63 cl	photosynthesis	yes	Eckert, 1978
P. sylvestris (Scotch pine)	3 cl	photosynthesis	yes	Börtitz and Vogl, 1965
	6 seedlings	photosynthesis	yes	Lorenc-Plucinska, 1982
		photorespiration		
Zea mays (maize)	7 lines, 2 cv	CO_2 compensation point		
		photosynthesis		
		respiration	yes	Grzesiak, 1979
Enzyme Activity and Isoenzymes				
Lolium perenne (perennial ryegrass)	3 cl	glutamate synthetase activity	yes	Wellburn et al., 1981
	2, 4 cl	nitrite reductase activity	no	
Picea abies (Norway spruce)	18 cl	protein bands	no	Braun, 1977d
Pinus strobus (eastern white pine)	63 cl	acid phosphatase activity	yes	Eckert, 1978
		acid phosphatase isoenzymes	yes	
	36 cl	esterase isoenzymes	no	Houston, 1970; Houston and Stairs, 1972
	36 cl	peroxidase activity	no	Houston, 1970; Houston and Stairs, 1972
	36 cl	peroxidase isoenzymes	yes	Houston, 1970; Houston and Stairs, 1972
	63 cl	peroxidase isoenzymes	no	Eckert, 1978
P. sylvestris (Scotch pine)	23 cl, 4 seedlings	phenoloxidase isoenzymes	no	
		L-leucine amino-pipidase isoenzymes	no	Mejnartowicz et al., 1978
	2 pop	GPT, GOT activity	yes	Horsman and Wellburn, 1977
		RuDPC activity	yes	
		peroxidase activity	yes	
Hydrocarbon Emissions				
Cucumis sativus (cucumber)	2 cv	ethane[b]	yes	Bressan et al., 1979
Cucurbita pepo (squash, pumpkin)	2 cv	ethane[b]	yes	Bressan et al., 1979
Hordeum vulgare (barley)	2 cv	ethylene	no	Baba and Sakai, 1976
Pigment Content				
Euphorbia pulcherrima (poinsettia)	17 cl	flavonol	no	Krizek and Semeniuk, 1981
Lolium perenne (perennial ryegrass)	2 cl	anthocyanins	no	Bell and Mudd, 1976
		chlorophyll		
Picea abies (Norway spruce)	resistant vs. sensitive	chlorophyll	yes	Schindlbeck, 1977
	12 cl	chlorophyll	no	Braun, 1977d

(continued)

Table 5 (continued)

Species	Comparison[a]	Parameter	Resistance Correlation	Reference
		Other Parameters		
Lolium perenne (perennial ryegrass)	3 cl	ATP formation	yes	Wellburn et al., 1981
Muhlenbergia asperifolia	2 pop	sulfur assimilation	yes	Campbell, 1972
Petunia hybrida (petunia)	3 cv	leaf water potential	no	Elkiey and Ormrod, 1979c
Picea abies (Norway spruce)	resistant vs. sensitive	protein synthesis	no	Schindlbeck, 1977
		thioester content	yes	
		sulfhydryl compound content	yes	
		protein synthesis	no	
	18 cl	sulfur distribution	no	Braun, 1977d
		organic sulfur	yes	
		sulfhydryl content	yes	
	16 cl	water potential	yes	Braun, 1977c, 1978
		water content	yes	
Pinus strobus (eastern white pine)	59 cl	phenol content	yes	Eckert, 1978
		polyphenol content	yes	
		monoterpene content	no	
	36 cl	phenol content	yes	Houston, 1970; Houston and Stairs, 1972
P. sylvestris (Scotch pine)	9 cl	specific gravity	no	Patton, 1981

[a] Abbreviations: cl (clones), cv (cultivars), pop (populations).

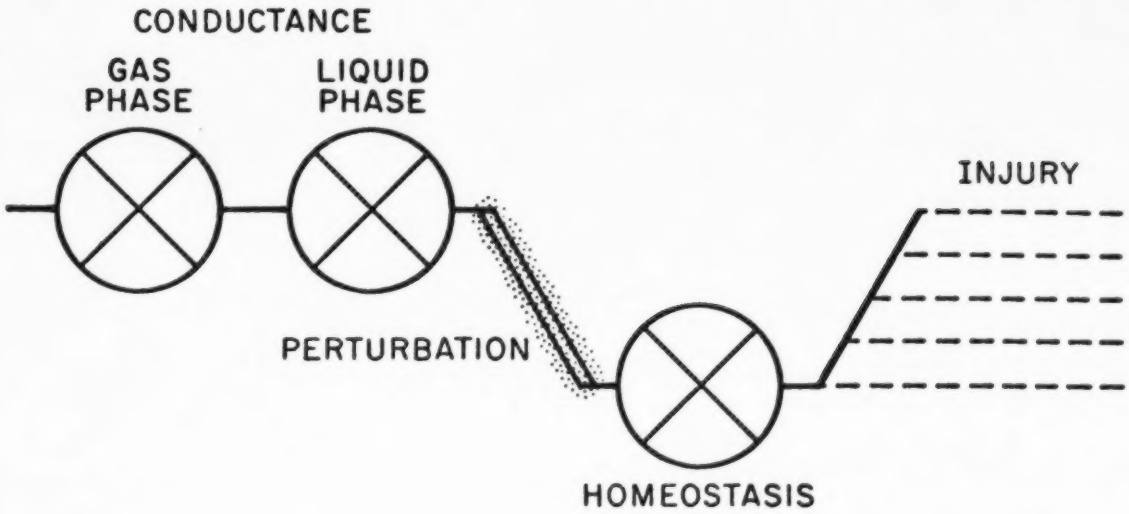
[b] Based on sensitivity to bisulfite with the assumption that bisulfite sensitivity paralleled sulfur dioxide sensitivity.

Figure Legends

Figure 1. Conceptual model of metabolic processes determining plant response to sulfur dioxide; major processes regulating plant variation are gas and liquid phase conductance and homeostasis (adapted from Tingey and Taylor, 1982).

Figure 2. Analog model and representative leaf cross section describing the relationships between sulfur dioxide flux and leaf conductances (g).

Figure 3. Pathways for sulfur dioxide metabolism and potential detoxification. The question mark indicates that the occurrence of a nonphotochemical process oxidizing sulfite to sulfate is uncertain.



Conceptual Model of Plant Response to SO_2

Figure 1. Conceptual model of metabolic processes determining plant response to sulfur dioxide; major processes regulating plant variation are gas and liquid phase conductance and homeostasis (Tingey and Taylor, 1982).

DETERMINANTS OF SULFUR DIOXIDE FLUX (J)

$$J_{SO_2} = (C_a - C_l) \cdot (g_a + g_s + g_r)$$

GAS PHASE

PATHWAY CONDUCTANCE

Conductances (g_L)

Boundary layer (g_a)

Stomata (g_s)

Concentration Gradient (ΔC)

Ambient conc. (C_a)

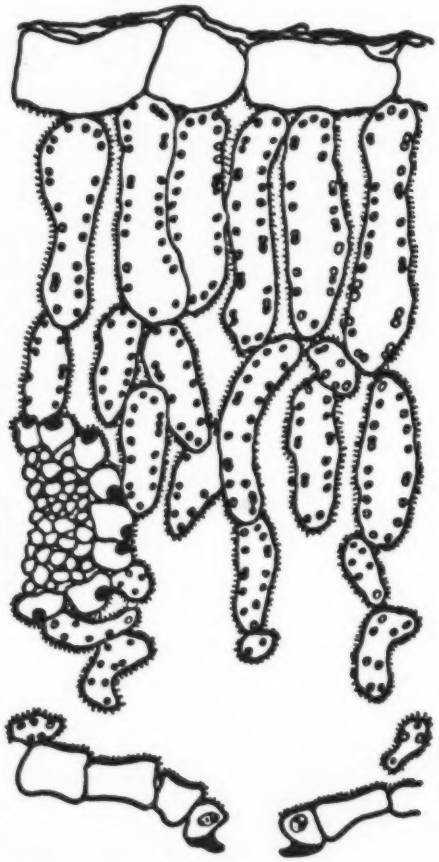
Gas-to-liquid conc. (C_l)

Flux

Leaf surface flux ($J_{Surface}$)

Leaf interior flux ($J_{Internal}$)

$J_{Total} = J_{Internal} + J_{Surface}$



LIQUID PHASE

PATHWAY CONDUCTANCE

Conductance

Residual/Chemical/Mesophyll (g_r)

Chemical Potential Gradient (ΔC)

Gas-to-liquid concentration ($H_m C_l$)

Perturbation site concentration (C_p)

Intermediate concentration (C_e)

Figure 2. Analog model and representative leaf cross section describing the relationships between sulfur dioxide flux and leaf conductances (g).

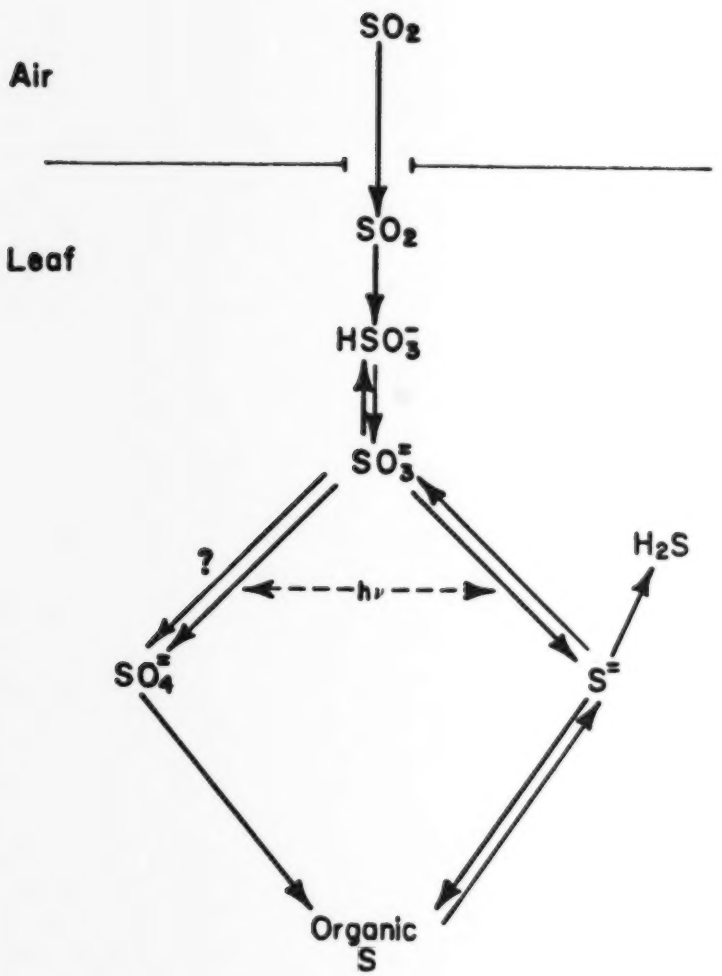


Figure 3. Pathways for sulfur dioxide metabolism and potential detoxification. The question mark indicates that the occurrence of a nonphotochemical process oxidizing sulfite to sulfate is uncertain.